EFFECT OF FLOCK SIZE ON FORAGING ACTIVITY IN WINTERING SANDERLINGS

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Birds in flocks may increase the proportion of time spent feeding and thus food intake by dividing the time spent watching for predators among flock members. This advantage of foraging in flocks has been supported by mathematical analysis (Pulliam 1973) and by experimental work with aviary birds (Powell 1974). Field work with Wood Pigeons (*Columba palumbus*) (Murton et al. 1971) showed that single birds had lower feeding rates and spent more time looking around than flock birds, but Murton (1971) interpreted this as indicating that single birds were seeking to join flocks for reasons unrelated to predator protection. Page and Whitacre (1975) found that predation is substantial on wintering shorebirds and that they are less susceptible to predation when in flocks, but no evidence exists that flocking shorebirds increase their foraging activity. To test this possibility, we examined foraging activity in relation to flock size in wintering Sanderlings (*Calidris alba*). Because Barash (1974) found that chickadees in flocks have fewer aggressive encounters than single birds, we looked for similar behavior among Sanderlings.

METHODS

Data were collected by 9 investigators from 26 to 28 November 1974 at Punta Santa Rosa 37 km northwest of Kino, Sonora, Mexico. The beaches on the south side of the point are sandy while those on the north, at the mouth of a channel, are composed of algae-covered rocks approximately 4–6 cm in diameter. Sanderlings were the most common shorebirds present.

Investigators dispersed along the beaches in 4 groups. Each group consisted of 1 recorder and 1 or 2 observers; group members and roles were changed frequently. Each group was equipped with a spotting scope, stopwatch, mechanical counter, and binoculars. The first bird observed in a flock was selected by counting back from the lead bird using random numbers less than 10. Successive birds were picked by counting back a random number from the position of the last bird observed. When the count exceeded the number of remaining birds, counting continued with the lead bird. For purposes of analysis we decided to take approximately equal numbers of observations of birds in 3 classes on rocky and sandy beach: singles, flocks of 2–10 shorebirds, and flocks of greater than 10. Shorebirds other than Sanderlings were included in the total flock size, since all birds contribute to the possible reduction of predator alert time.

We recorded the total seconds out of 1 min that a Sanderling appeared to be foraging (hereafter called foraging time). The observer timed foraging activity with a stopwatch while the recorder monitored 1 min intervals. We also recorded the number of feeding movements in 1 min (hereafter called foraging rate) using a mechanical counter. To test for possible differences in foraging method due to substrate type or flock size, we

TABLE 1

FORAGING TIMES* OF SANDERLINGS IN DIFFERENT FLOCK SIZES ON DIFFERENT HABITATS

	Flock size								
	Singles			2–10			> 10		
Habitat	N	$\bar{x}$	s^2	N	$\bar{x}$	s^2	N	$\bar{x}$	s^2
Sandy	33	53.8	79.0	54	49.3	191.0	67	53.3	151.0
Rocky	34	49.9	67.6	45	51.1	157.3	55	53.2	90.7
Combined	67	51.8	75.8	99	50.1	174.7	122	53.3	122.9

* Total seconds in 1 min spent foraging.

classified foraging movements as probes if the bill penetrated the surface, or pecks if it did not. We estimated the number of movements on the few occasions that they were too rapid to be counted directly. Thirty-two of the total 475 min of foraging data include birds observed between 30 and 45 sec whose rates were prorated to 1 min. No sleeping birds or birds observed for less than 30 sec were included in the data analysis. Aggressive interactions were recorded only for those birds selected for foraging observations.

Due to large variances, we transformed the data as the square root of $(\times + .5)$ to normalize them for statistical tests. Statistical analysis was done with the aid of the University of Arizona computer services using the SPSS statistics programs.

RESULTS

Sanderling flocks on sandy beaches tended to be small and move rapidly whereas those on rocky beaches were slower and sometimes large enough to include both sleeping and foraging birds. We collected no quantitative data on the relative frequency of flock sizes, but flocks of 2 to 10 birds seemed most common. Single birds were fairly common but usually did not remain single for long before being joined by others.

There was no appreciable change in mean time spent foraging due to par-

TABLE 2

FORAGING RATES* OF SANDERLINGS IN DIFFERENT FLOCK SIZES ON DIFFERENT HABITATS

	Flock size								
	Singles			2–10			> 10		
H bitat	N	$\bar{x}$	s^2	N	$\bar{x}$	s^2	N	$\bar{x}$	s^2
Sandy	28	26.9	401.4	40	51.0	1708.3	31	37.8	881.8
Rocky	22	43.7	627.8	41	57.0	889.9	25	61.9	1832.4
Combined	50	34.3	561.1	81	54.1	1287.0	56	48.6	1426.4

* Number of movements per minute.

Table 3

Polynomial Analysis of Variance—Foraging Rate with Flock Size on Sandy Beach

Source	Degrees of freedom	M. S.
Between	2	25.54*
Linear Term	1	10.33
Quadratic Term	1	42.05*
Within	96	5.32

* F probability $< .05$

ticipation in flocks by Sanderlings (Table 1). Analysis of variance showed no significant relationship between flock size and foraging time in either habitat (sandy $P = .22$, rocky $P = .54$) or in both combined ($P = .22$).

However, the foraging rate of Sanderlings in flocks ($\bar{X} = 51.8$) was considerably higher than that of single birds ($\bar{X} = 34.3$), and this difference was significant by a 1-tailed t-test ($t = 3.15$, $P = .001$). The increase in foraging rate was not associated with a change in foraging method. Of a sample of 504 movements by single birds, 92% were probes, while 90% of 7091 movements by birds in flocks were also probes.

Mean foraging rate tended to increase as flock size increased on rocky beach (Table 2), but this trend was not significant by analysis of variance ($P = .48$). There was a marked decline of foraging rate in flocks greater than 10 on sandy beach, shown to be significant by polynomial analysis of variance (Table 3). Mean foraging rates of birds on rocky beach were higher in all cases than on sandy beach (Table 2). This difference was significant by a 2-tailed t-test for single birds ($t = 2.93$, $P = .005$) and very nearly so for flocks ($t = 1.97$, $P = .051$). Ninety % of foraging movements were probes on both rocky and sandy beach ($N = 2111$ and 5484 respectively).

We found a positive correlation between aggressions per bird-minute and flock size ($r = .212$, significance of $r = .0001$). Increased aggressive in-

Table 4

Aggressions of Sanderlings in Different Flock Sizes on Different Habitats

Habitat	Flock size		
	Singles	2–10	>10
Sandy	.076* (53)	.122 (90)	.376 (96)
Rocky	.019 (53)	.092 (76)	.100 (80)

* Aggressions per bird observed per minute. Number of bird-minutes in each category in parentheses.

teractions in larger flocks were due to increased aggressions per bird (Table 4) and increased numbers of birds participating. Aggressions were more frequent in all size classes on sandy beach.

DISCUSSION

The increased foraging rate of Sanderling in flocks is equivalent to increased food intake if the proportion of successful feeding movements remains relatively constant, as Goss-Custard (1970a) found for Redshank (*Tringa totanus*). We attribute the lack of a corresponding increase in foraging time to our inability to measure the brief pauses between foraging movements.

The increased foraging rate of Sanderlings in flocks could be attributed to causes other than less time spent looking for predators. Krebs (1974) suggested that herons in flocks fed at a faster rate than solitary individuals because flocks form at patches of abundant food. However, Sanderling flocks and single birds foraged in the same areas and flocks moved cohesively along the beach. Murton (1971) and Krebs (1974) have argued that single birds spend less time foraging because they are searching for flocks to join. This seems unlikely in the case of Sanderlings since flocks were seldom far from foraging single birds. Finally, Sanderlings in this study did not change their foraging method when in flocks to achieve the increase. We conclude that increased foraging rate may be related to less time spent searching for predators between feeding movements.

Our data indicate that Sanderlings do not join flocks to reduce aggressive encounters, as Barash (1974) found for chickadees. Recher and Recher (1969) found that Semipalmated Sandpipers (*Calidris pusilla*) likewise increase aggressive encounters in flocks.

The decreased foraging rate of birds in large flocks on sandy beach did not occur on rocky beach and may have been caused by limited food on sandy beach. Sanderlings on sandy beach had lower feeding rates, more aggressive encounters, and higher flock speed than those on rocky beach, suggesting that food was less abundant on sandy beach. Higher aggression among shorebirds has been associated with lower food availability (Recher and Recher 1969), as has higher flock speed of woodland passerines (Morse 1970). Large flocks on habitats with limited resources may deplete locally available prey thereby reducing the average feeding rate (Goss-Custard 1970b). Protection from predators does not diminish as flock size increases, but competition for food where resources are limited may determine an optimum flock size.

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